

## Plant responses to livestock grazing frequency in an Australian temperate grassland

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Livestock grazing is often thought to enhance native plant species co-existence in remnant grasslands but may also favour exotic invaders. Recommendations for appropriate grazing strategies are needed, for which an understanding of the response of plant species is necessary. We explored the response of plant species and plant functional groups to grazing in temperate grassland of the Monaro Tablelands of south-east Australia by comparing species abundance in adjacent areas that differed in livestock grazing regime (minimal, infrequent and frequent). We also examined whether species with similar responses to grazing share certain traits and consider whether these traits might provide a useful method of assessing grazing impact. At the scale measured (0.25 m<sup>2</sup>), an infrequent grazing regime maximised plant species co-existence in these grasslands due to widespread invasion by exotic plant species at infrequent grazing intensity. Many native species declined in abundance when grazing frequency increased from minimal to infrequent. Annuals invaded under infrequent grazing while perennials declined most strongly under high frequency grazing. Low levels of grazing apparently reduce cover and create sites suitable for seed recruitment whereas more frequent grazing reduces the persistence of perennials. While there was a tendency for native species to be more susceptible to grazing impact than exotics, plant traits, in particular longevity (perennial, annual) provided a better prediction of the response of plants to grazing. Although a few native plant species persisted at high grazing frequency, even infrequent livestock grazing may not be appropriate for the conservation of many native perennial grassland species. Targeted reductions in grazing frequency may be necessary to enable the long-term coexistence of grazing susceptible species.

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The native grasslands of temperate southern Australia have been depleted of native plant species and modified by livestock grazing, cultivation, fertiliser addition and intentional and accidental plant introductions over the past 200 yr (McDougall and Kirkpatrick 1993, Benson 1994). Formerly, these grasslands were subject to grazing by native marsupials (e.g. kangaroos) and emus, and occasionally burned. Hunting by aboriginal people and dingos probably limited populations of those native

herbivores. Since the 1830s fire has been suppressed, ungulate livestock (especially sheep) have been kept at much higher grazing intensities and spatially constrained by fences since the 1870s (Hancock 1972). The shift to frequent grazing by ungulates is generally considered to be the cause of most of the vegetation change, and appropriate grazing regimes are being sought that will conserve native species. It has been argued that the decline of native plant species has been the result of an

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absence of pre-adaptations to intensive ungulate grazing impacts (Fox and Fox 1986, McIntyre and Lavorel 1994b) and therefore plant origin (native vs exotic) may be useful in identifying grazing resistance or resilience traits (Allcock and Hik 2003).

While intensive grazing can result in reductions in native plant species richness (McIntyre and Lavorel 1994b, Prober and Thiele 1995, Fensham 1998), species coexistence is also thought to decline in the absence of grazing (Tremont 1994). Intermittent grazing has been argued to be compatible with the conservation of many native species (Tremont 1994, Fensham 1998, McIvor 1998, McIntyre and Martin 2001) and is therefore the basis of conservation management strategies in many remnant temperate Australian grasslands. This is consistent with non-equilibrium theories of plant species coexistence (e.g. Connell and Slatyer 1977, Connell 1978, Huston 1979, Denslow 1985, Huston and DeAngelis 1994, but see Mackey and Currie 2001). It has been hypothesised that grazing reduces the competitive effects of palatable, dominant or tall-statured species enabling shorter or less palatable species to establish, thereby increasing coexistence (Belsky 1992, Tremont 1994, Damhoureyeh and Hartnett 1997, Gough and Grace 1998).

Grazing also influences patterns of species richness and coexistence via alterations to species persistence, seed production and rates of colonisation (Gibson and Brown 1991, Olf and Ritchie 1998). While grazing can increase the likelihood of local extinction through reductions in survival and seed production, particularly of tall palatable species (O'Connor 1991a, Hodgkinson 1992), grazing can also increase rates of gap formation and reduce litter, favouring plant establishment (O'Connor 1991b) and increasing species richness (Foster and Gross 1998). These mechanisms may favour small, ephemeral, gap colonising species (Biddiscombe et al. 1954, Moore 1959, Moore and Biddiscombe 1964, Belsky 1992) and in regions where many such species are present, ungulate grazing will most likely increase local plant species richness (Milchunas et al. 1988, Noy-Meir et al. 1989).

In temperate Australia species rich native grassland remnants typically occur within a matrix of pastures as small, isolated areas with high edge to area ratios, such as road verges, railway reserves and travelling stock reserves (McDougall and Kirkpatrick 1993). More extensive, although less species rich, native grasslands persist as pastures grazed by livestock (McIntyre and Lavorel 1994b). Conservation of grassland communities across the landscape will therefore be largely dependent on finding appropriate grazing strategies for these areas.

If widespread species or syndromes of traits that are consistently sensitive to grazing impacts can be identified, then these could be used to monitor vegetation condition and the suitability of grazing regimes. One

such syndrome is longevity (e.g. indeterminate polycarpic perennial vs determinate monocarpic annual or biennial). Identification of grazing sensitive traits is useful for developing hypotheses of how vegetation change occurs, predicting species responses, and inferring past grazing impacts from the species composition of a community (McIntyre and Lavorel 2001).

In this paper, patterns of plant species richness, responses of individual species and patterns of plant traits and origins are examined across fence-lines with contrasting grazing frequency. The study was undertaken to test the following hypotheses: 1) plant species richness is maximised under infrequent grazing regimes; 2) native plant species are more likely to decline than exotics in response to frequent ungulate grazing and 3) a few key plant traits or syndromes can explain much of the response to ungulate grazing.

## Methods

### Geology, climate and vegetation

This study was undertaken in grassland on the basalt plain of the Monaro Tablelands of southern New South Wales, Australia. The basalt plain extends south from Cooma (36°14'S, 149°10'E) for ca 80 km towards Bombala (37°00'S, 149°14'E) in an unbroken belt 40 km in width. The undulating landscape varies in altitude from 800 to 1150 m a.s.l. The lack of tree cover on the plain is apparently as a result of prior climate and fire regimes and maintained by low soil moisture availability in the clay rich soils and livestock grazing (Cambage 1909, Costin 1954, Benson 1994, Tulau 1994).

Annual rainfall tends to increase in a south-easterly direction across the basalt plain with a low of ca 500 mm at Cooma (average for 1858–1982) to the north of the study region to 700 mm at Nimmitabel (average for 1894–1996) in the south-east. Rainfall is slightly higher in summer. Temperatures are cold in winter (Cooma: June mean minimum  $-2^{\circ}\text{C}$ , mean maximum  $11^{\circ}\text{C}$ ) and although summers can be short, they are often hot (Cooma: January mean minimum  $11^{\circ}\text{C}$  and mean maximum  $28^{\circ}\text{C}$ ). Typically plant growth is limited by cold in winter and water deficit in summer.

Where exotic perennial pastures have not been sown, the vegetation is dominated by tall, sward or tussock-forming, native grass species (e.g. *Poa sieberiana*, *Themeda australis*, *Austrostipa scabra* and *Austrostipa bigeniculata*) with a phylogenetically diverse forb flora occurring in inter-tussock spaces (Costin 1954, Benson 1994, Dorrrough 2001). Exotic annual grass species (e.g. *Vulpia* spp. and *Bromus* spp.) and exotic legumes (*Trifolium* spp. and *Medicago* spp.) are also widespread and abundant.

## Site selection and field survey

Where long-term differences in grazing management are known, contrasting vegetation across fences has proved to be an effective means of determining community and individual plant species responses to differences in grazing regime (Noy-Meir et al. 1989, Fensham et al. 1999). Fences on the Monaro Tablelands were mostly constructed 50–120 yr ago, following bearings rather than topographic or soil variation, and therefore can provide a direct comparison of contrasting long-term management regimes with few confounding soil effects. Three contrasting grazing regimes were identified on the Monaro: frequent (natural pastures on properties), infrequent (travelling stock reserves) and minimal (roadside verges). Frequently grazed pastures are generally set-stocked, year-round, at 3–6 dry sheep equivalents (dse) ha<sup>-1</sup> (a single non-lactating ewe is one dse) (Anon. 1996, Garden et al. 2000). Infrequently grazed reserves are typically stocked <20 d yr<sup>-1</sup>, with an average annual dse ha<sup>-1</sup> of between one and three although densities can be high for short periods of time. Minimally grazing sites are ungrazed, except during drought when livestock may be herded along roads. Most frequently grazed properties have a 40–50 yr history of occasional spreading clovers and fertilisers (gypsum and sulphur fortified superphosphate), however the majority of fertiliser has been applied to disturbed sown pastures (Garden et al. 2000) which were not sampled in this study. In addition since these applications were often aerial, adjacent roadsides and reserves were likely to have been subject to drift (Muir 1978). Prior unpublished research by the authors suggests that there is little variation in soil nutrients between areas with frequent (12 sites), infrequent (6 sites) and minimal (4 sites) grazing (phosphorous (mg/kg)  $F_{2,19} = 0.28$ ; total nitrogen (%)  $F_{2,19} = 1.22$ ; sulphur (mg/kg)  $F_{2,19} = 0.82$ ; ammonium nitrate (mg/kg)  $F_{2,19} = 0.41$ ) although sheep camps and sown pastures were typically more nutrient rich (Dorrough, 2001). Pastures that had been cultivated and sown with exotic perennial grasses and annual legumes were not surveyed.

Roadsides are the only spatially well replicated areas consistently ungrazed by livestock on the Monaro basalt grasslands. Roadsides are often subject to disturbance from machinery (vehicles and road works) and increased drainage and this, rather than a lack of livestock grazing, may influence vegetation composition (McIntyre and Lavorel 1994a). For this reason, roadsides were only sampled if they were wider than 5 m, had no signs of mechanical physical disturbance or recent grazing, and were not subject to drainage from the adjoining road. Road maintenance often involves mowing of up to 2 m of roadside vegetation adjoining the road and quadrats were placed to avoid these zones (see below). No roadsides on lower slopes satisfied the drainage or

disturbance criteria so the survey only included mid and upper slopes.

All sites surveyed in this study occurred on the Tertiary derived basalt plateau as mapped on the Bega 1:250 000 Metallogenic Map (Barnes and Herzberger 1975). Twenty sites were selected from across the region where a fence-line separated more frequently grazed areas (M) from less frequently grazed areas (L): the “side” effect. The sites were classified into three “grazing contrasts”: 1) frequent (M)–minimal (L): 10 sites; 2) frequent (M)–infrequent (L): 4 sites; 3) infrequent (M)–minimal (L): 6 sites.

The degree of independence between roadside sites on the same road is difficult to ascertain. Two rules for independence of roadside sites were set. Firstly, adjacent sites along a road were separated by a minimum of 500 m and, secondly, adjacent roadside sites were also separated by a change in topography such as a gully or ridgeline. The final twenty sites selected were broadly distributed across the basalt plain, with few sites occurring within one kilometre of each other. Field surveys were conducted between the 4 and 20 November 1998 (late spring) when most species are flowering. On each side of the fence a 20 m transect was laid out and ten 0.5 × 0.5 m quadrats were located at 2 m intervals. On roadsides, transects were normally 2–3 m from the fence or road edge, and 3–10 m from the fence in reserves and pastures to avoid grazing effects caused solely by spatial proximity to a fence-line. The presence and visually estimated cover abundance of each plant species, litter, rock and bare ground were recorded in each quadrat by a single observer. The vegetation stature (cm) was measured with a rising plate meter (200 cm<sup>2</sup>, 250 g) at the centre of each quadrat. In every second quadrat soil depth was estimated to a depth of 0.5 m using a soil auger.

## Plant traits

Seven plant traits were recorded for all species present at three or more grazing contrasts (Appendix 1). Data for the traits were recorded using available literature (Cunningham et al. 1981, Auld et al. 1987, Harden 1990, Tremont 1994, McIntyre et al. 1995, Lunt and Morgan 1999) and field observations. The plant traits of all plant species recorded in more than three grazing contrasts, are shown in Appendix 1.

Assessment of plant height was based on average plant height observed in an ungrazed situation on the Monaro basalts, rather than maximum height possible for that species within its range. Criteria for vegetative spread were based on gap filling ability rather than on vegetative reproduction alone. Species able to spread and fill space successfully, even if this does not entail production of daughter ramets, were scored as having

partial vegetative ability. For example tussock grasses that produce numerous basal daughter tillers (e.g. *Poa sieberiana*) and trailing plants (e.g. *Einaridia nutans*) were scored as having partial vegetative ability. Three types of dispersal were recognised; wind, animal and undefined. Plants were recorded as animal dispersed if they could adhere to skin or hair or produced edible fruits. Preliminary analysis suggested that grazing responses did not differ between species with wind or undefined dispersal mechanisms and so only two dispersal mechanisms (animal and other) were used in final analyses.

## Statistical analyses

Species richness patterns and physical site attributes (e.g. bare ground, soil depth) were analysed using mixed model Restricted Maximum Likelihood (REML) variance components analysis (Corbeil and Searle 1976) undertaken using Genstat 5.0 (Anon. 1987). REML analyses allow the specification of fixed and random model structures for the analysis of unbalanced data sets that are unsuitable for analysis of variance. In all models grazing frequency (minimal, infrequent and frequent) was the fixed effect while the random model consisted of side (L or M) nested within site and quadrat nested within side.

Few individual species were present at all grazing contrasts and none were present in all quadrats. Analysis of individual species responses was therefore conducted on transect level means. At each site, for each species present,  $\log_{10}$  (average cover abundance + 1) was calculated for the transect on each side of the fence-line and the value for the less grazed side (L) was subtracted from that of the more frequently grazed (M), ( $\approx \log_{10} [\text{Cover}_M] - \log_{10} [\text{Cover}_L]$ ). If a species was absent from both sides of the fence-line contrast it was treated as missing data, rather than having a value of zero. The value obtained for each species at each site is an index of whether it increases (positive score), is unaffected (zero score) or decreases (negative score) in response to the grazing contrast. Mean responses across sites for each species in each of the three grazing contrasts and the overall mean across all sites were calculated, provided the species was present at  $\geq 3$  sites. The significance of individual species responses for each grazing contrast was examined using a t-test to determine whether, on average, the species responses differed from zero.

Analyses of the relationship between plant traits and grazing responses (grazing contrasts and overall) were conducted using Generalised Linear Models in Genstat 5.0 (Anon. 1987). Null models were initially constructed and individual terms added in a forward stepwise manner until no further additions lead to significant changes in deviance ( $p > 0.05$ ). Importance of individual

terms in final models was determined by removing each remaining term from the full model.

## Results

### Physical site attributes

Litter cover and vegetation stature significantly declined with an increase in grazing frequency (Table 1). Relationships with bare ground and soil depth were non-significant, although there was a trend for increasing bare ground from minimal to infrequent and frequent grazing. The lack of a soil depth effect suggests that the grazing contrasts were not confounded by soil gradients.

### Species richness

Grazing management explained significant variation in total ( $\chi^2 = 12.4$ ;  $p < 0.001$ ), native ( $\chi^2 = 13.1$ ;  $p < 0.001$ ) and exotic ( $\chi^2 = 17.0$ ;  $p < 0.001$ ) species richness. Total species richness was highest in infrequently grazed sites due to increases in the richness of exotic species along the minimal to infrequent contrast, and declines in the richness of natives between infrequent and frequent grazing (Table 2). As a result minimally and frequently grazed sites had similar total species richness, but their composition differed markedly.

### Individual species responses

Of the 120 plant species recorded in the surveys, only seven species were recorded in  $> 50\%$  of quadrats. These were the native species *Poa sieberiana* (86%), *Themeda australis* (58%), *Austroanthonia linkii* (55%) and *Asperula conferta* (51%) and the exotics *Vulpia* spp. (62%), *Trifolium striatum* (55%), and *Medicago minima* (50%).

Table 1. Changes in deviance and predicted means for REML models of bare ground, litter, vegetation structure and soil depth. Values for bare ground and litter are means of their ranked classes. Least significant differences (lsd) at  $p < 0.05$  are presented. Models include the explanatory term Grazing Frequency with two degrees of freedom and a random model structure as described in the text. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

Variable	Deviance	Means			lsd
		Minimal	Infrequent	Frequent	
Bare ground	4.5	1.7	2.4	2.2	0.7
Litter	29.8***	3.5	2.9	2.5	0.3
$\log_{10}$ vegetation stature (cm)	15.5***	1.9	1.4	1.4	0.2
$\log_{10}$ soil depth (cm)	2.0	2.4	2.2	2.3	0.2

Table 2. Changes in deviance and predicted means for REML models of total, native and exotic plant species richness  $0.25 \text{ m}^{-2}$  in minimal, infrequent and frequently grazed grassland. Least significant differences ( $p < 0.05$ ) are presented. Models include the explanatory term Grazing Frequency with two degrees of freedom and a random model structure as described in the text. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

Variable	Deviance	Means			lsd
		Minimal	Infrequent	Frequent	
Total species	12.4**	12.6	15.7	11.7	2.0
Native species	13.1**	7.8	8.6	5.0	1.9
Exotic species	17.0**	4.8	7.1	6.7	1.0

The majority of species were uncommon, and 88 (73%) were recorded in <10% of quadrats.

Species with consistent significant responses to grazing in any of the three grazing contrast treatments or with significant overall mean values are shown in Appendix 1. A total of 48 species varied significantly in abundance due to grazing in at least one grazing frequency contrast. Of these, 30 species declined and 17 species increased in response to increasing grazing frequency. Only one species (*Carex inversa*) had significant conflicting responses to grazing in different contrasts.

### Plant traits and response to grazing

Plant traits were significantly correlated with grazing responses in the overall contrast and the two minimal grazing contrasts (Table 3). Longevity was the major explanatory variable in these models (Table 3). In all three contrasts perennial species were predicted to have negative responses to increasing grazing frequency while annual species responses were positive (Fig. 1). In addition to longevity, growth form was found to be significant in models for minimal – frequent contrasts (Table 3). On average, grasses were more likely to respond positively to grazing than forbs (Fig. 2). Plant height was also weakly correlated (but significantly so) with grazing response for the minimal – frequent

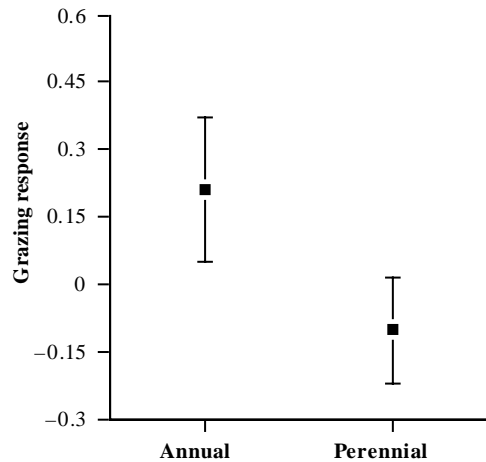


Fig. 1. Mean response of perennial and annual plant species across minimal – frequent grazing contrasts. Positive values indicate an increase in abundance due to grazing. Bars are two times the standard error. Predicted means were calculated holding all other terms in the model constant.

contrasts (Table 3) with taller plants tending to respond more negatively to grazing (Fig. 3). Dispersal mechanism was significant only in the model of overall response to grazing. Species that possessed animal dispersed seeds were more likely to respond positively than other species. (Table 3; Fig. 4). Although plant origin was significant when added singly to models it was never significant when other terms were included.

### Discussion

This study showed that invasion by exotic plant species occurs at even low grazing frequency, whereas many native species become scarce at high grazing frequency. Total species richness, therefore, peaked at infrequent grazing, as was predicted from other studies in similar vegetation in Australia (McIntyre and Lavorel 1994a, b, Pettit et al. 1995, Fensham et al. 1999) and elsewhere (Milchunas et al. 1988). However, native species richness

Table 3. Significant variables in each of four models describing the grazing responses of individual grassland species. Models are generalised linear regressions with identity link and normal error distribution. Estimates of  $R^2$ , the variance ratio (F), degrees of freedom (DF) and probability (p) for the overall models are also shown.

Variable	DF	F	p
Overall $n = 80$ , $R^2 = 0.20$ , $F_{2,76} = 10.95$ , $p < 0.001$			
Longevity	1	17.1	<0.001
Dispersal (animal, other)	1	5.1	<0.05
Minimal – Infrequent $n = 44$ , $R^2 = 0.20$ , $F_{1,41} = 11.76$ , $p = 0.001$			
Longevity	1	12.0	<0.001
Minimal – Frequent $n = 49$ , $R^2 = 0.26$ , $F_{5,42} = 4.47$ , $p = 0.002$			
Longevity	1	9.1	<0.01
Growth Form	1	6.5	<0.05
Height	3	2.2	<0.1
Infrequent – Frequent $n = 23$			
No significant terms			

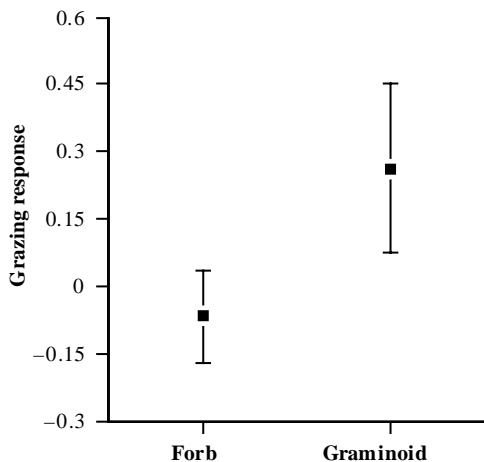


Fig. 2. Mean response of forb and graminoid plant species across minimal – frequent grazing contrasts. Positive values indicate an increase in abundance due to grazing. Bars are two times the standard error. Predicted means were calculated holding all other terms in the model constant.

was as high in the least grazed (minimal frequency) sites as in the infrequently grazed reserves and several native perennial inter-tussock forb species declined in abundance across the minimal-infrequent contrast. While it has been argued that moderate levels of disturbance may be necessary for the conservation of many native grassland taxa (Lunt 1991, Gilfedder and Kirkpatrick 1994) little support could be found for this in the current study. The different conclusion in this study could be the result of differences in grazing regimes or of differences in the plant communities and habitat. The minimal grazing sites still receive some grazing from kangaroos, although

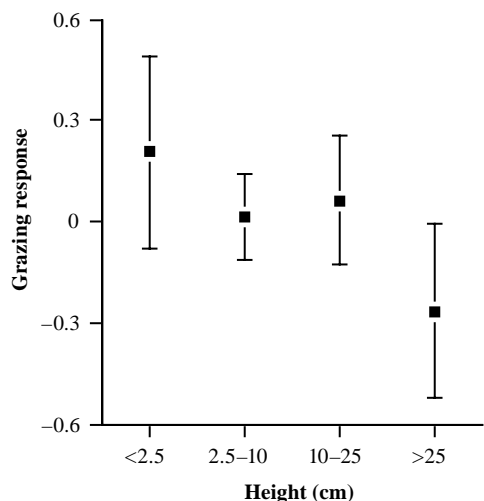


Fig. 3. Mean response of plant species of different potential height across minimal – frequent grazing contrasts. Positive values indicate an increase in abundance due to grazing. Bars are two times the standard error. Predicted means were calculated holding all other terms in the model constant.

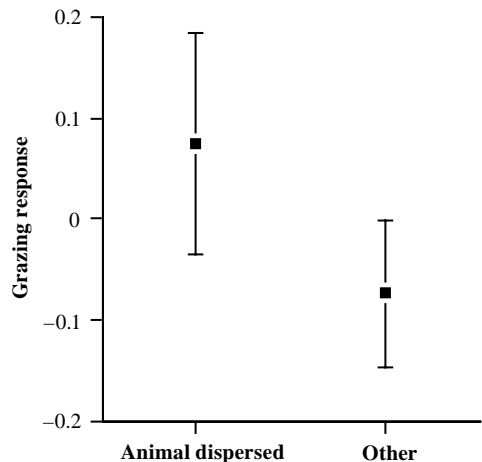


Fig. 4. Mean response of plant species with different dispersal mechanisms across all grazing contrasts. Positive values indicate an increase in abundance due to grazing. Bars are two times the standard error. Predicted means were calculated holding all other terms in the model constant.

rarely, and occasionally from stock. Also, the habitats surveyed were of relatively low productivity, excluding lower slopes that often support large dominant grasses that could exert strong competitive effects if they are not grazed (Proulx and Mazumder 1998). However, these results suggest that even the infrequent livestock grazing regime favours exotic invasion while not obviously benefiting native persistence.

### Individual species responses to grazing

Of the 120 species recorded in this study, one third were too infrequent for a grazing response to be tested, and of the remainder slightly more than half were positively or negatively sensitive to grazing. This is a substantially greater proportion than has been observed in Australian sub-tropical grasslands (Fensham 1998), although, it is similar to Australian arid rangelands (Landsberg et al. 1997). The reasons for such variation in the response of individual plant species and entire communities to grazing are difficult to determine, and may reflect differences in methodology, and the impacts and evolved responses to grazing history (McIntyre and Martin 2001), rainfall (Moore 1970), drought (Landsberg et al. 1999), fire (Gill et al. 1981), resource availability (Proulx and Mazumder 1998) and vegetation composition (Vesk and Westoby 2001).

Although the fence comparisons undertaken in this study clearly reflected differences in grazing regimes, up to 100 yr of livestock grazing preceded the erection of many of the fences. Some of the more grazing sensitive native species were perhaps rare or locally extinct before the fenced roadsides and reserves were established. Without local refugia these species may have failed to

recolonise the minimally grazed habitats. Therefore, despite the high proportion of grazing sensitive species observed in this study, of the persisting species, those most threatened by grazing impacts are likely to be rare and the probability of determining a grazing response may be low.

### Plant traits and response to grazing

Long-term grazing may influence plant communities firstly by acting as a selective filter eliminating intolerant species and secondly through the evolution of persisting species. Grazing history may therefore influence the ability of a community to respond to environmental changes, including changes in grazing intensity (Mack and Thompson 1982, Milchunas et al. 1988). Geographic isolation of the Australian continent during the Tertiary period allowed a diverse fauna of "soft-footed" marsupials and ratite birds to evolve (Flannery 1994). Many of the larger species (megafauna) went extinct 11 000–25 000 yr before present, perhaps shortly after human occupation (Flannery 1990, Davis 1996). Low productivity, limited water availability, hunting by aboriginal people and dingos (a human introduction), a managed fire regime and the absence of large herbivores possibly prevented sustained grazing pressure during the last few thousand years. Introduction of ungulate livestock in the early 19th century resulted in changes in both the frequency and intensity of herbivore grazing.

Exotic grassland species from other continents have evolved under ungulate grazing regimes and may therefore have pre-adaptations to cope with the current grazing regimes in Australia, whereas the native species may be at a disadvantage (McIntyre and Lavorel 1994b). On the Monaro Tablelands the high abundance of exotic species in pastures and their lesser prominence in habitats with less ungulate grazing supports this hypothesis. However, this was the result of a few species, and some exotics declined with intense grazing and some natives resisted grazing. Rather than origin, a clearer pattern emerged with life history traits, especially longevity. Annuals, and the few biennials, were much more successful in more frequently grazed habitat, whereas perennials were less successful. Since the majority of exotics were annual or biennial and the vast majority of natives were perennial ( $n = 80$ , likelihood ratio,  $\chi^2 = 39.7$ , 1 DF,  $p < 0.001$ ) this suggests that longevity and associated traits were conferring much of the apparent advantage on exotics.

Differences between perennial and annual species in response to grazing are widely recognised (Pidgion and Ashby 1940, Noy-Meir et al. 1989, Wilson 1990, Fensham et al. 1999). Increasing grazing pressure has many effects that favour species with a shorter lifecycle, such as increased rates of gap creation, redistribution of

nutrients (Hilder and Mottershead 1963) and higher rates of nutrient cycling (Chaneton et al. 1996), particularly close to the soil surface. Many annuals are small statured, and this also appears to be an important trait for persisting under heavy grazing. Small stature may reduce the ability of grazing animals to detect plants leading to lower levels of herbivory on flowers, seeds and leaves.

In Mediterranean Europe where intensive grazing and cultivation are long-standing practices, the flora may be locally diverse, although composed predominantly of annual species (Shmida 1981) which are favoured by grazing (Noy-Meir et al. 1989). Even within these communities, increasing disturbance and grazing results in a shift among annuals towards those with a shorter life cycle (Fernandez et al. 1993).

The success of annuals relative to perennials under frequent grazing may also be influenced by climate. In most years on the Monaro Tablelands the winter-spring period is suitable for plant growth and provides a sufficient season for annuals to complete their life cycle, and allocate all available resources to seed production. The native perennials include C3 pathway species that also grow and produce seed in winter-spring, but they allocate substantial resources to vegetative spread, storage, persistent underground structures, and to maintaining durable foliage (at the expense of specific leaf area) over summer. The C4 pathway perennials are similar except that they do not reach maximum growth or reproduce until the hotter conditions in summer, when their higher water use efficiency also enables them to cope relatively better with dry periods. In the absence of heavy grazing the perennial life history allows species to make use of episodes of soil moisture following summer rains as well as the more prolonged winter soil moisture. Provided that grazing does not destroy the foliage of perennials over summer they can compete successfully with annual species that may have higher assimilation rates. Under infrequent and minimal grazing a high cover of foliage leads to thatch or litter blanketing the soil which may prevent seed of many species from either germinating or establishing, favouring long-lived and vegetatively reproducing species.

Grazing in winter-spring may impact similarly on both perennials and annuals, depending on their palatability. As conditions become drier, as in drought, the remaining foliage becomes subject to increasing grazing pressure if herbivore populations are maintained, and as drought typically occurs over summer perennials are most affected. Grazing and trampling by ungulates during periods of moisture stress also generate bare ground suitable for seedling establishment once moisture availability increases. Since annuals allocate more biomass to seeds (Chapin III 1980), annuals could dominate seedling recruitment. The year-round grazing of pastures by stock combines most of the grazing regime char-

acteristics described above: a recipe for driving the community from perennial towards annual dominance. Since the climate and prior grazing regime apparently favoured native perennials, there are few native annuals available to take their place when grazed, instead exotic annuals from equivalent habitats in other continents come pre-adapted to occupy these frequently grazed grasslands.

Other than longevity, the traits growth form (grass or forb) and dispersal mechanism (animal dispersed or other) were important in one model with grasses and species with animal dispersed seeds tending to be most abundant at higher grazing frequency. Other studies have found grasses to be more tolerant of grazing than broad-leaved forb species (Pettit et al. 1995, but see McIntyre and Lavorel 2001), although the later typically make up the majority of species in many species rich grasslands (Tremont and McIntyre 1994). Many declining native and exotic species are tall perennial inter-tussock forb species and tall, palatable forb species have been found to benefit from reduced grazing pressure (Wahren et al. 1994). In our study only three grasses declined with increasing grazing frequency and the only native species to increase in abundance were grasses (*Bothriochloa macra* and *Austrostipa scabra*).

Active dispersal via grazing animals may be an important character allowing plants to capitalise on gaps created by grazing or to enable re-colonisation following frequent and heavy grazing. Particularly in the case of those able to survive ingestion, seed may be deposited in nutrient enriched locations that are highly suitable for establishment (Malo and Suarez 1995).

Although simple traits were important predictors of grazing response, they were still only able to explain ca 20% of the variation in species responses. The within species response to grazing is often variable and responses between species within trait and taxonomic groups can also be highly variable. For example two of the species with consistent responses due to frequent grazing are exotic annual legumes in the genus *Trifolium*. One of these species increases due to grazing (*T. striatum*), the other declines (*T. arvense*). Traits that were not measured such as relative growth rate, palatability, growth season, seed number and seed bank persistence may be important in further understanding response to grazing (O'Connor 1991a, Cocks 1992, Rogers 1993, Reader 1998, McIntyre et al. 1999).

## Conservation management

On the Monaro Tablelands infrequent and frequent livestock grazing appears to have led to the decline in abundance and richness of certain perennial plant species. Reduced richness and abundance of native plant species is of particular concern. Strategies for conserving

native plant biodiversity in grazed grasslands should consider the identity and functional traits of those species present and consideration should be given to developing grazing strategies for broader areas of the landscape that enable grazing intolerant species to persist. While minimally grazed sites are important for the conservation of plant communities dominated by intolerant species, they are frequently narrow and potentially subject to many external influences (weed invasion, nutrient enrichment, disturbance). The best options for conserving many intolerant species may be in other areas of the broader landscape. While grazing intolerant species are less abundant in infrequently or frequently grazed pastures, reducing grazing intensity and frequency in grassland adjoining roadsides may provide additional opportunities for persistence and recruitment of declining plant species.

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Appendix 1. Plant responses to increasing grazing frequency and plant functional traits for grassland plant species observed in  $\geq 3$  sites. Grazing responses are across minimal – infrequent (1), minimal – frequent (2), infrequent – frequent (3) grazing frequency contrasts and the mean response across all contrasts (overall). Negative values indicate declines in plant abundance. Grazing responses in bold differ significantly from 0 ( $p < 0.1$ ). Functional traits shown are origin (N = native, E = exotic), longevity (P = perennial, A = shortlived annual or biennial), growth form (F = forb, G = graminoid), lifeform (H = Hemicryptophyte, C = Chamaephyte, P = Phanerophyte, T = Therophyte, G = Geophyte), height (1 =  $< 0.025$  m, 2 =  $0.025$ – $0.1$  m, 3 =  $0.1$ – $0.25$  m, 4 =  $> 0.25$  m), seed dispersal (1 = animal dispersed, either by adhesion or ingestion, 2 = wind dispersed, 3 = other) and vegetative spread (N = no, P = partial, Y = yes).

Species	Grazing response				Plant traits						
	1	2	3	Overall	Origin	Longevity	Growth form	Life form	Height	Dispersal	Vegetative
<i>Acaena ovina</i>	-0.158	<b>-0.28</b>	<b>-0.345</b>	<b>-0.26</b>	N	P	F	H	3	1	N
<i>Aira caryophylla</i>	0.182		<b>-0.384</b>	-0.11	E	A	G	T	2	1	N
<i>Ajuga australis</i>		<b>-0.26</b>		<b>-0.29</b>	N	P	F	H	2	3	N
<i>Arenaria serpyllifolia</i>	<b>0.306</b>			<b>0.31</b>	E	A	F	T	2	3	N
<i>Arthropodium milleflorum</i>				-0.34	N	P	F	H	3	3	N
<i>Asperula conferta</i>	-0.464	<b>-0.41</b>	-0.058	<b>-0.36</b>	N	P	F	C	2	3	Y
<i>Austrodanthonia linkii</i>	0.085	0.042	0.046	<b>0.18</b>	N	P	G	H	3	1	N
<i>Austrostipa scabra</i>		<b>0.41</b>		<b>0.45</b>	N	P	G	H	4	1	N
<i>Bothriochloa macra</i>		<b>0.819</b>		<b>0.56</b>	N	P	G	H	3	1	P
<i>Brachyscome heterodonta</i>		0.005		-0.04	N	P	F	H	3	3	Y
<i>Brachyscome rigidula</i>		<b>-0.21</b>		<b>-0.24</b>	N	P	F	H	2	2	P
<i>Bromus hordeaceus</i>	<b>0.389</b>	<b>0.407</b>	0.27	<b>0.37</b>	E	A	G	T	2	1	N
<i>Capsella bursa-pastoris</i>		<b>0.606</b>		<b>0.47</b>	E	A	F	T	2	1	N
<i>Carex breviculmis</i>	<b>-0.536</b>			<b>-0.46</b>	N	P	G	H	3	3	Y
<i>Carex inversa</i>	<b>0.344</b>	-0.097	-0.406	-0.04	N	P	G	H	2	3	Y
<i>Cerastium glomeratum</i>	<b>0.245</b>	0.153	-0.258	0.10	E	A	F	T	2	3	N
<i>Chrysocephalum apiculatum</i>	0.237	-0.173		-0.06	N	P	F	H	3	2	P
<i>Cirsium arvense</i>	0.218	-0.0094		0.08	E	A	F	T	4	2	N
<i>Convolvulus erubescens</i>	-0.093	-0.1		-0.05	N	P	F	H	2	3	P
<i>Crassula sieberiana</i>	-0.029	0.082	-0.058	0.01	N	A	F	T	1	3	N
<i>Craspedia variabilis</i>	-0.009			<b>-0.12</b>	N	P	F	H	4	2	N
<i>Critesion leporinum</i>		<b>0.298</b>		0.34	E	A	G	T	2	1	N
<i>Daucus glochidiatus</i>	0.096	0.152		0.06	N	A	F	T	2	1	N
<i>Desmodium varians</i>		0.128		<b>0.18</b>	N	P	F	H	2	1	P
<i>Dichelacne crinita</i>				<b>-0.31</b>	N	P	G	H	4	1	N
<i>Dichondra repens</i>				0.08	N	P	F	H	1	3	Y
<i>Einadia nutans</i>				0.14	N	P	F	C	1	1	P
<i>Elymus scaber</i>	-0.053	-0.126	-0.06	-0.09	N	P	G	H	3	1	N

Appendix 1. (Continued).

Species	Grazing response				Plant traits						
	1	2	3	Overall	Origin	Longevity	Growth form	Life form	Height	Dispersal	Vegetative
<i>Epilobium billardieri</i>		-0.166		<b>-0.14</b>	N	P	F	H	3	2	Y
<i>Erodium cicutarium</i>		<b>0.655</b>	<b>0.64</b>	<b>0.69</b>	E	A	F	T	1	1	N
<i>Erodium crinitum</i>				<b>0.22</b>	N	P	F	H	2	1	P
<i>Erophila verna</i>		0.41	<b>-0.518</b>	0.13	E	A	F	T	1	3	N
<i>Geranium solanderi</i>	0.336	<b>-0.564</b>	-0.364	<b>-0.28</b>	N	P	F	H	2	3	P
<i>Glycine clandestina</i>		-0.031		-0.05	N	P	F	C	2	3	P
<i>Gnaphalium sph. (Euchiton)</i>	0.295			0.08	N	P	F	H	2	2	Y
<i>Gypsophila australis</i>				0.06	N	A	F	T	1	3	N
<i>Hydrocotyle laxiflora</i>				<b>-0.46</b>	N	P	F	H	2	3	Y
<i>Hypericum gramineum</i>	0.132			-0.02	N	P	F	H	2	3	N
<i>Hypochaeris radicata</i>	0.002	<b>-0.436</b>	<b>-0.57</b>	<b>-0.31</b>	E	P	F	H	3	2	N
<i>Leptorhynchus squamatus</i>				<b>-0.50</b>	N	P	F	H	3	2	P
<i>Leucopogon fraseri</i>				<b>-0.29</b>	N	P	F	H	3	2	N
<i>Linaria arvense</i>	0.0225	-0.12		-0.16	E	A	F	T	2	3	N
<i>Lolium perenne</i>	-0.193	<b>0.499</b>		0.15	E	P	G	H	3	3	N
<i>Luzula flaccida</i>	<b>-0.198</b>			<b>-0.26</b>	N	P	G	H	2	3	N
<i>Medicago minima</i>	0.226	0.14	<b>-0.37</b>	0.03	E	A	F	T	2	3	P
<i>Medicago polymorpha</i>		<b>0.159</b>		0.03	E	A	F	T	2	1	P
<i>Myosotis discolor</i>		<b>-0.367</b>		<b>-0.31</b>	E	A	F	T	2	1	N
<i>Oreomyrrhis eriopoda</i>	0.246			0.12	N	P	F	H	3	3	N
<i>Oxalis perennans</i>	0.016	-0.097	-0.135	-0.06	N	P	F	H	2	3	Y
<i>Petrorhagia nanteuilli</i>	0.33	0.057	-0.112	0.10	E	A	F	T	2	3	N
<i>Pimelea glauca</i>				-0.07	N	P	F	C	3	3	N
<i>Plantago lanceolata</i>	-0.381			<b>-0.52</b>	E	P	F	H	3	3	N
<i>Plantago varia</i>	-0.027	<b>-0.402</b>		<b>-0.21</b>	N	P	F	H	3	3	N
<i>Poa pratensis</i>	0.082	<b>0.299</b>		<b>0.22</b>	E	P	G	H	3	3	Y
<i>Poa sieberiana</i>	-0.083	<b>-0.257</b>	-0.466	<b>-0.25</b>	N	P	G	H	4	3	P
<i>Polygala japonica</i>				<b>-0.32</b>	N	P	F	H	2	3	N
<i>Ranunculus lappaceus</i>				<b>-0.18</b>	N	P	F	H	3	1	N
<i>Rumex acetosella</i>	-0.01	<b>-0.3</b>	-0.064	-0.15	E	P	F	H	2	3	Y
<i>Rumex dumosus</i>		0.077		0.11	N	P	F	H	4	1	N
<i>Salvia verbenaca</i>	-0.032	0.07		0.14	E	P	F	H	3	3	N
<i>Schoenus apogon</i>				-0.12	N	A	G	T	1	3	N
<i>Scleranthus biflorus</i>	0.209			0.03	N	P	F	C	1	3	Y
<i>Scleranthus diander</i>		-0.311		-0.17	N	P	F	H	1	3	Y

## Appendix 1. (Continued).

Species	Grazing response				Plant traits						
	1	2	3	Overall	Origin	Longevity	Growth form	Life form	Height	Dispersal	Vegetative
<i>Solenogyne gunnii</i>	0.33	0.157	-0.283	0.09	N	P	F	H	1	3	N
<i>Stackhousia monogyna</i>				<b>-0.61</b>	N	P	F	H	3	3	N
<i>Swainsona behriana</i>		-0.159		-0.11	N	P	F	H	2	3	P
<i>Taraxacum officinale</i>	0.02			0.05	E	P	F	H	3	2	N
<i>Themeda australis</i>	<b>-0.422</b>	<b>-0.94</b>	<b>-0.798</b>	<b>-0.76</b>	N	P	G	H	4	1	P
<i>Tragapogon dubium</i>		<b>-0.427</b>		<b>-0.26</b>	E	A	F	H	4	2	N
<i>Trifolium arvense</i>	0.04	<b>-0.182</b>	<b>-0.679</b>	<b>-0.19</b>	E	A	F	T	2	1	P
<i>Trifolium glomeratum</i>				0.20	E	A	F	T	2	1	P
<i>Trifolium repens</i>	0.09			0.03	E	A	F	T	2	3	P
<i>Trifolium striatum</i>	<b>0.485</b>	<b>0.603</b>	0.228	<b>0.49</b>	E	A	F	T	2	1	P
<i>Trifolium subterraneum</i>				<b>0.85</b>	E	A	F	T	2	3	P
<i>Veronica</i> sp.	<b>-0.337</b>			<b>-0.34</b>	N	P	F	C	2	3	N
<i>Viola betonicifolia</i>				<b>-0.23</b>	N	P	F	H	2	3	N
<i>Vittadinia cuneata</i>				0.08	N	P	F	H	3	2	N
<i>Vittadinia muelleri</i>	0.178	0.28		0.23	N	P	F	H	2	2	N
<i>Vulpia</i> sp.	<b>0.683</b>	<b>0.771</b>	<b>0.287</b>	<b>0.65</b>	E	A	G	T	2	1	N
<i>Wahlenbergia communis</i>	-0.124	-0.244		-0.14	N	P	F	H	3	3	N
Mean	0.06	0.01	-0.19	-0.03							